

## S38-4 The effect of environmental conditions on early growth in geese

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**Abstract** Geese, one of the few avian herbivores, face a combination of unique constraints during growth. Goslings must feed by themselves; they must reach a large size during a short growing season; they grow in the Arctic under harsh climatic conditions; and, despite their high nitrogen requirement for growth, they feed only on plants, which are low in protein. We examined how these constraints shape growth strategy in the greater snow goose (*Anser caerulescens atlanticus*). Growth rates of goslings are among the highest reported in precocial birds. Goslings maintain a very high resting metabolic rate throughout growth and are fully competent homeotherms soon after hatching: they seem to prioritize maintenance of optimum internal conditions for biosynthetic activity over energy conserving strategies. Such an expensive life-style can only be sustained by feeding at a very high rate on high-quality food. The consequence is that growth rate is highly sensitive to environmental conditions encountered in early life. Although the developmental pattern in goslings shows some phenotypic plasticity when environmental conditions deteriorate, it is not sufficient to compensate for factors such as a seasonal decline in plant quality. Therefore, goslings that hatch late or grow slowly must fledge at a smaller size, and this may have serious fitness consequences for survival and adulthood.

**Key words** Snow geese, Growth, Food, Thermoregulation

### 1 Introduction

One of the most important factors affecting growth patterns in birds is the developmental mode of the hatchling, i.e. the altricial-precocial spectrum (Starck and Ricklefs, 1998). Geese are precocial birds that have been the focus of some growth studies, although they have been ignored in comparisons of altricial-precocial birds. Yet geese are subject to a series of unique ecological circumstances that affect their growth patterns different from other precocial birds. Here we review some of these factors and how they affect the energetics and growth patterns in geese, using our research on greater snow geese (*Anser caerulescens atlanticus*) as a case study.

Geese are one of the few herbivorous groups of birds (Sedinger, 1997). Because of the relatively low quality of their diet (low protein, high fiber), herbivores must hold large quantities of food in the gut for long periods for digestion. These conditions, however, are incompatible with the avian digestive system which is small in volume and short in retention time to minimize mass. That is why herbivory is found in so few bird taxa, such as grouse and ratites, which are large in body and poor flyers or flightless. Geese are also relatively large in body but are unique in having retained the capacity for strong flight. Consequently, the goose alimentary system is typically avian with limited digestive capacity. To cope, geese have developed behavioral adaptations to improve nutrient uptake, such as discriminating food selection, prolonged feeding time and long

migrations to exploit highly seasonal environments such as the Arctic.

Breeding in the Arctic confers some advantages, such as access to high quality food and almost continuous daylight for feeding during the summer. It also imposes severe constraints. The Arctic is a cold and windy environment, and subjects goslings to high thermoregulatory costs. Although the relatively large body size of goslings may provide some thermoregulatory relief, it also lengthens the growth period, which is a major constraint where summers are short. The most severe constraint faced by goslings, however, is undoubtedly their strictly herbivorous diet. This is unusual, as the chicks of most leaf- or seed-eating birds are fed on an animal diet (e.g., insects) to meet their high energy and protein requirements. Therefore, a herbivorous diet is likely to impose a strong limitation on growth in geese.

### 2 Growth rates in geese

Despite being herbivorous and self-feeding, goslings also have remarkably high growth rates (Aubin et al., 1986; Sedinger, 1986; Lesage and Gauthier, 1997). In Table 1, we compare the growth constant of the logistic equation ( $K$ ), an index of growth rate, for a number of goose species. Ricklefs (1979) described the relationship between  $K$  (logistic growth constant) and  $M$  (asymptotic body mass) in birds by the following allometric equation:

$$K = 1.10M^{-0.34}.$$

We used this equation to calculate the value of  $K$  predicted ( $K_{\text{pred}}$ ) for each species in Table 1. Among the 14 studies compared, all but two reported higher empirical growth rates than predicted by the equation, which is surprising because the allometric equation is based largely on altricial birds that should have higher growth rates than precocial birds. These results suggest that selective pressure for fast growth is very strong in geese.

Goslings achieve very high growth rates despite their well-developed legs and mobility from hatching, which have their own energy costs. In greater snow geese, for example, we found that the more mature organs at hatching, such as legs, gizzard and gut, developed early and grew more rapidly than other parts of the body (Lesage and Gauthier, 1997; also Sedinger, 1986). Such results indicate that embryonic constraints at the tissue level are not the primary factor limiting growth rate in geese, as predicted by the tissue-allocation hypothesis (Ricklefs et al., 1994).

### 3 Metabolic rate and energy expenditure of goslings

In order to grow, the balance between energy intake and energy expenditure for maintenance must be positive. For a self-feeding precocial bird in the Arctic, maintenance of metabolic rate is likely to be high and dependent on environmental conditions. As the expenditure side of the equation increases, surplus energy may decrease if not matched by an increase in food intake, and thus lead to retarded growth.

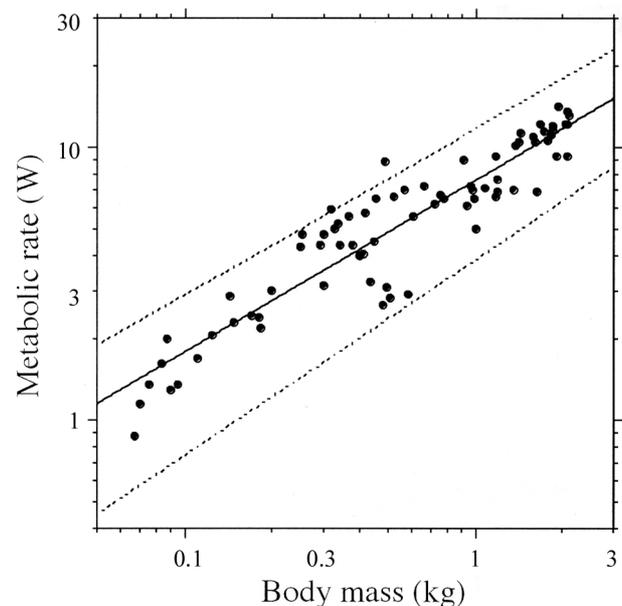
We conducted experiments on the metabolism of captive-reared goslings hatched from eggs collected in the wild. Over 1 to 40 days, we exposed them to various ambient temperatures and measured  $O_2$  consumption,  $CO_2$  production, and internal body temperature ( $T_b$ ; Ratté, 1998). We also evaluated the cost of thermoregulation using heated taxidermic mounts of goslings of 4 different ages (5, 10, 20 and 30 days; Fortin et al., 2000b). The mounts were calibrated in the laboratory using live goslings, and then exposed to field conditions in the Arctic to measure heat loss under various environmental conditions (temperature, wind, and solar radiation; Renaud, 1999).

One- to two-day old goslings maintained their  $T_b$  at around  $39.7^\circ\text{C}$  when exposed for 1 hour to temperatures ranging from  $5$  to  $25^\circ\text{C}$  (Ratté, 1998). At  $-5^\circ\text{C}$ , however, they had difficulty, as their  $T_b$  dropped to  $37.8^\circ\text{C}$  over the same period; but by day 10 this had been overcome (Ratté, 1998). Under field conditions, four day old goslings living in average air temperatures of  $7.7^\circ\text{C}$  already have a  $T_b$  of  $40.4^\circ\text{C}$ , very close to that of adults (Fortin et al., 2000a). Therefore, newly-hatched goslings are fully homeothermic and able to maintain their  $T_b$  near adult values over a wide range of environmental conditions, as has been observed in other Anatidae (Visser, 1998).

In line with their high  $T_b$ , goslings also have high thermoneutral metabolic rates at rest (RMR). Throughout

growth, the RMR of goslings is more than twice the predicted basal metabolic rate (BMR) of adult birds of similar size (Fig. 1). It should be noted that the RMR of growing goslings, unlike the BMR of adults, includes the cost of biosynthesis for growth. The RMR of neonate goslings 1–2 days old (body mass: 77 g) already averages  $1.25\text{ W}$  (Fig. 1), just over twice the value predicted for nonpasserine adults of similar size (Lasiewski and Dawson, 1967). This is the highest reported RMR value for neonates, even when compared to such cold-hardy neonates as common eiders, *Somateria mollissima* (Steen and Gabrielsen, 1986). Peak metabolic rate (PMR) of goslings, defined as the metabolic rate at  $-5^\circ\text{C}$ , is also very high, averaging  $1.5 \times \text{RMR}$ , or  $3.8 \times \text{BMR}$  of adult birds of similar size (Fig. 1).

Despite their high RMR, goslings are exposed to significant thermoregulatory costs as average air temperature during the growth period at our study site on Bylot Island, Nunavut, Canada ( $73^\circ\text{N}$ ,  $80^\circ\text{W}$ ) is only  $5.7^\circ\text{C}$  (Renaud, 1999). The corresponding standard operative temperature, an effective environmental temperature that takes the influence of wind and solar radiation into account ( $T_{\text{es}}$ ; Bakken, 1976), is only  $5.3^\circ\text{C}$ . This value declines with the season from  $11.3^\circ\text{C}$  at hatching to  $1.1^\circ\text{C}$  at 40 days of age. These temperatures are well below the thermoneutrality zone of goslings, as their lower critical temperature is  $15\text{--}20^\circ\text{C}$  (Ratté, 1998). Regulatory, cold-induced thermogenesis therefore represents a significant portion of energy expenditure in goslings. Using heated taxidermic mounts calibrated on live goslings, Renaud (1999) estimated that thermogenesis represented on average 31% of the maintenance metabolism of



**Fig. 1** Relationship between resting metabolic rate (RMR) or peak metabolic rate (PMR) and body mass of greater snow goose goslings

RMR is the solid line, measured at  $25^\circ\text{C}$ , within the thermoneutrality zone; PMR is the upper stippled line, measured at  $-5^\circ\text{C}$ . The lower stippled line is the predicted basal metabolic rate for adult non-passerine birds of similar size (from Lasiewski and Dawson, 1967).

growing goslings between 1 and 40 days of age: 42% in newly hatched goslings, declining to 22% at day 40.

Self-feeding in goslings clearly imposes very high maintenance costs. In particular, their high RMR is probably an adaptation that enables individuals to sustain a high growth rate. High PMR also allows them to maintain a high  $T_b$  during cold periods, as foraging goslings do not commonly use hypothermia as an energy-saving mechanism (Fortin et al., 2000a). Thus they must prioritize the maintenance of optimum internal conditions for biosynthetic activity over strategies of energy conservation.

#### 4 Food intake, food quality and body growth

Such an expensive life-style can only be sustained by feeding intensively on high-quality food. Yet even though food quality is high in the Arctic, there is much evidence that growth rate in geese is commonly food-limited. In an experiment where captive goslings were reared in the field, those that received a high quality food-supplement grew faster and were larger at fledging (Lindholm et al., 1994). Similarly, Lepage et al. (1998) found a direct and positive correlation between the availability of high quality food and growth in wild goslings.

Plants begin a steep seasonal decline in quality, with dropping protein, around the time of gosling hatching (Manseau and Gauthier, 1993; Lepage et al., 1998). Even

though regrowth of grazed plants may be of high quality, this may not be sufficient to compensate for the reduction of biomass due to grazing (Piedboeuf and Gauthier, 1999). Goslings hatched earlier in the season thus exploit higher food quality than those hatched later; hence they grow faster (Sedinger and Flint, 1991; Cooch et al., 1991; Lepage et al., 1998). Because of the short Arctic summer, goslings that hatch late may not be able to complete their growth, and as a result survive less well during the following autumn migration (Schmutz, 1993; Cooch, 2002); those that do survive become small adults (Cooch et al., 1991).

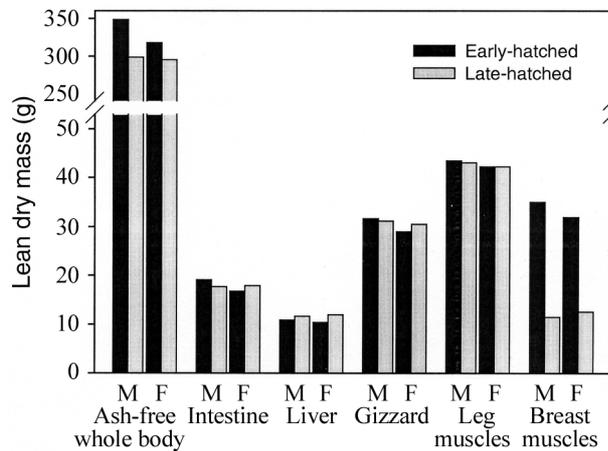
Given the serious fitness consequences of reduced growth rate, it could be expected that late-hatched, slow-growing goslings may adjust their growth pattern to maximize their chances of fledging. This we examined by collecting goslings shortly before fledging and comparing organ development between early- and late-hatched goslings (Lesage and Gauthier, 1998). Late-hatched goslings carried less total body protein than those hatched early (Fig. 2). Deficiency was greatest in breast muscle, indicating that when faced with a diminished food supply, goslings prioritize development of the energy supply organs (digestive tract, legs) over other organs such as wings.

In a laboratory experiment, we also examined the effect of variations in food quality on growth, digestive efficiency and organ development. We found that diet quality had a strong effect on growth (Fig. 3). Even though food intake was higher for the goslings on low-quality food, this

**Table 1** Growth coefficients in geese

Species	Env.	Sex	Body mass	$K_{obs}$	$K_{pred}$	Reference
<i>Anser caerulescens caerulescens</i>	W	-	1 890	0.151	0.085	Aubin et al., 1986
	C	-	1 890	0.115	0.095	Ankney, 1980
<i>Anser caerulescens atlanticus</i>	W	M	2 666	0.096	0.075	Lesage and Gauthier, 1997
	W	F	2 391	0.090	0.078	Lesage and Gauthier, 1997
	C	-	2 525	0.132–0.168	0.077	Lindholm et al., 1994
	C	-	2 525	0.112–0.131	0.077	Fournier (unpubl. data)
<i>Anser anser</i>		M	3 400	0.098	0.069	Heinroth and Heinroth, 1928 (in Starck and Ricklefs, 1998)
		F	2 930	0.109	0.073	Heinroth and Heinroth, 1928 (in Starck and Ricklefs, 1998)
<i>Anser indicus</i>	W	-	2 600	0.065	0.076	Würdinger, 1975 (in Sedinger, 1992)
	C	-	2 600	0.094	0.076	Würdinger, 1975 (in Sedinger, 1992)
<i>Branta canadensis atlantica</i>	C	-	3 800	0.079	0.067	Würdinger, 1975 (in Sedinger, 1992)
<i>Branta canadensis moffitti</i>	C	M	5 075	0.075	0.061	Yokum and Harris, 1966
	C	F	4 111	0.068	0.065	Yokum and Harris, 1966
<i>Branta canadensis minima</i>	W	M	1 341	0.106	0.095	Sedinger, 1986
	W	F	1 223	0.120	0.098	Sedinger, 1986
<i>Branta bernicla nigricans</i>	W	-	1 237	0.081	0.098	Sedinger and Flint, 1991
<i>Branta bernicla orientalis</i>	C	-	1 273	0.125	0.097	Morehouse, 1974 (in Sedinger, 1992)
Domestic goose	C	M	3 640	0.095	0.068	Laird, 1965 (in Ricklefs, 1973)
	C	F	3 750	0.078	0.067	Laird, 1965 (in Ricklefs, 1973)

Growth constant,  $K$ , from the logistic curve and minimum winter body mass, Env. = environment (W = wild, C = captivity),  $K_{obs}$  = observed value,  $K_{pred}$  = predicted value by allometric equation.



**Fig. 2** Lean dry mass of various organs and ash-free lean dry mass of whole body in early- and late-hatched male (M) and female (F) greater snow goose goslings collected shortly before fledging on Bylot Island

$n = 24$  for each combination of hatch period and sex. All values are standardized to a common value of total body ash to correct for differences in body size and age at capture (details in Lesage and Gauthier, 1998).

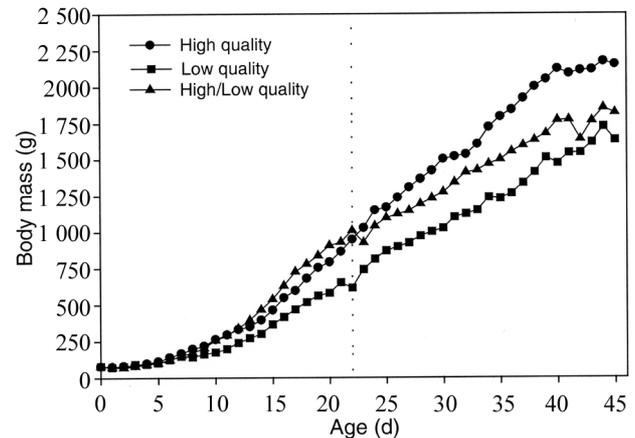
was not sufficient to prevent a slowing of growth rate. At the end of 45 days, goslings reared on a low-quality diet for all or part of the experimental period had enlarged digestive organs and reduced breast muscles compared to goslings reared for the entire period on a high-quality diet.

Overall, these experiments show that goslings can adapt their developmental pattern to mediate the impact of a decreasing food quality. Despite these adjustments, however, it appears that the capacity of goslings to buffer the effects of variations in food quality are limited, probably because their gut is always working near maximum capacity (Manseau and Gauthier, 1993).

## 5 Conclusion

Our results suggest that optimal allocation of energy and nutrients to growth and maintenance is critical for achieving high growth rates in young geese. Their self-feeding mode, herbivorous diet, and high maintenance costs are all ecological factors that nevertheless contribute to limiting growth rate. Although developmental patterns in goslings show some phenotypic plasticity when environmental conditions deteriorate, they are not enough to compensate for such factors as natural decline in plant food quality and availability. Thus, we conclude that growth rates in wild geese are limited more by environmental conditions than by embryonic constraints at the tissue level.

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**Fig. 3** Body mass of greater snow goose goslings reared on different diets as a function of age

The first group fed on high-quality diet (2/3 goose chow: 1/3 alfalfa,  $n = 6$ ), the second group fed on low-quality diet (1/3 goose chow: 2/3 alfalfa,  $n = 5$ ), and the third group started on high-quality diet but was switched to low-quality diet (stippled line) during the growth period ( $n = 5$ ).

## References

- Ankney CD, 1980. Egg weight, survival and growth of lesser snow goose goslings. *J. Wildl. Managmt.* 44: 174–182.
- Aubin AE, Dunn EH, MacInnes CD, 1986. Growth of lesser snow geese on arctic breeding grounds. *Condor* 88: 365–370.
- Bakken GS, 1976. A heat transfer analysis of animals, unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* 60: 337–384.
- Cooch EG, Lank DB, Dzubin A, Rockwell RF, Cooke F, 1991. Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology* 72: 503–512.
- Cooch EG, 2002. Fledging size and survival in snow geese timing is everything (or is it?). *J. Appl. Stat.* 29: 143–162.
- Fortin D, Gauthier G, Larochelle J, 2000a. Body temperature and resting behavior of greater snow goose goslings in the High Arctic. *Condor* 102: 163–171.
- Fortin D, Larochelle J, Gauthier G, 2000b. The effect of wind, radiation and body orientation on the thermal environment of greater snow goose goslings. *J. Therm. Biol.* 25: 227–238.
- Lasiewski RC, Dawson WR, 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13–23.
- Lepage D, Gauthier G, Reed A, 1998. Seasonal variation in growth of greater snow goose goslings: the role of food supply. *Oecologia* 114: 226–235.
- Lesage L, Gauthier G, 1997. Growth and organ development in greater snow goose goslings. *Auk* 114: 229–241.
- Lesage L, Gauthier G, 1998. Effect of hatching date on body and organ development in greater snow goose goslings. *Condor* 100: 316–325.
- Lindholm A, Gauthier G, Desrochers A, 1994. Effects of hatch date and food supply on gosling growth in arctic-nesting greater snow geese. *Condor* 96: 898–908.
- Manseau M, Gauthier G, 1993. Interactions between greater snow geese and their rearing habitat. *Ecology* 74: 2 045–2 055.
- Piedboeuf N, Gauthier G, 1999. Nutritive quality of forage plants for greater snow goose goslings when is it advantageous to feed on grazed plants? *Can. J. Zool.* 77: 1 908–1 918.
- Ratté J, 1998. Thermorégulation et croissance chez les oisons de la grande oie des neiges (*Chen caerulescens atlantica*). MSc Thesis. Quebec: Université Laval.

- Renaud M, 1999. Coûts énergétiques de la thermorégulation chez les jeunes de la grande oie des neiges en milieu naturel. MSc Thesis. Quebec: Université Laval.
- Ricklefs RE, 1973. Patterns of growth in birds. II Growth rate and mode of development. *Ibis* 115: 177–201.
- Ricklefs RE, 1979. Adaptation, constraint, and compromise in avian postnatal development. *Biol. Rev. Cambridge Phil. Soc.* 54: 269–290.
- Ricklefs RE, Shea RE, Choi IH, 1994. Inverse relationship between functional maturity and exponential growth rate of avian skeletal muscle a constraint on evolutionary response. *Evolution* 48: 1 080–1 088.
- Schmutz JA, 1993. Survival and pre-fledging body mass in juvenile emperor geese. *Condor* 95: 222–225.
- Sedinger JS, 1986. Growth and development of Canada goose goslings. *Condor* 88: 169–180.
- Sedinger JS, 1992. Ecology of pre-fledging waterfowl. In: Batt BDJ, et al. ed. *Ecology and Management of Breeding Waterfowl*. Minnesota: University of Minnesota, 109–117.
- Sedinger JS, 1997. Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. *Condor* 99: 314–326
- Sedinger JS, Flint PL, 1991. Growth rate is negatively correlated with hatch date in black brant. *Ecology* 72: 496–502.
- Starck JM, Ricklefs RE, 1998. Patterns of development in the altricial-precocial spectrum. In: Starck JM, Ricklefs RE ed. *Avian Growth and Development*. Oxford: Oxford University Press, 3–30.
- Steen JB, Gabrielsen GW, 1986. Thermogenesis in newly hatched eider (*Somateria mollissima*) and long-tailed duck (*Clangula hyemalis*) ducklings and barnacle goose (*Branta leucopsis*) goslings. *Polar Res.* 4: 181–186.
- Visser GH, 1998. Development of temperature regulation. In: Starck JM, Ricklefs RE ed. *Avian Growth and Development*. Oxford: Oxford University Press, 117–156.
- Yokum CF, Harris SW, 1966. Growth rates of Great Basin Canada geese. *Murrelet* 47: 33–37.